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SOCIAL ORGANIZATION WITHIN CLONES OF THE SEA ANEMONE *ANTHOPLEURA ELEGANTISSIMA*

LISBETH FRANCIS

University of Washington, Friday Harbor Laboratories, Friday Harbor, Washington 98250

The aggregating form of the anemone *Anthopleura elegantissima* often lives attached to large boulders and rocky outcroppings in closely packed groups. These are composed of genetically identical individuals, the products of asexual reproduction (Francis, 1973a). Contact between the tentacles of genetically different (non-clonemate) members of the species elicits aggression in one or both animals, while similar contact between clonemates is tolerated passively. Clonal aggregations remain separated from each other (Fig. 1) at least partly as a result of intraspecific aggression occurring at their adjacent borders (Francis, 1973b).

This aggressive behavior is rather elaborate, involving inflation of specialized effector organs, the blunt, white-tipped acrorhagi (Fig. 2), and stretching and bending movements of the oral disc and column that bring these turgid acrorhagi into contact with the non-clonemate adversary. During contact, scraps of the white acrorhagial ectoderm are applied to the body of the adversary where they adhere, slowly firing their batteries of large atrich nematocysts. Both the acrorhagi themselves and their large atrich nematocysts are deployed only during aggression (Ābel, 1954; Bonnin, 1964; Francis, 1973b). For an animal with a relatively limited behavioral repertoire and quite limited specialization of tissue types, this extensive investment in intraspecific aggression is remarkable.

In large clonal aggregations relatively few of the anemones are in a position to engage in battles at any given time. One might therefore expect the costs of intraspecific aggression to be distributed unevenly in such groups, with those animals at or near an interclonal border bearing more of the defense costs. To investigate this, I collected anemones from large, compact aggregations and compared individual size, sexual and asexual reproductive state, and acrorhagus size and number for animals from different locations within each clonal aggregation.

Materials and Methods

Collection, holding and anesthetization of specimens

The anemones were collected at low tide by gently prying the pedal discs free of the rock substratum. At Scripps Institute of Oceanography (SIO) and at the University of Washington's Friday Harbor Laboratories, the anemones were kept in bowls supplied with flowing sea water. They were anesthetized by replacing about half the sea water in each bowl with a 7% solution of magnesium sulphate, which was merely poured into the bowls. The anemones remained fairly well expanded during this process and most of them remained expanded without aeration or exchange of water during the two to twelve hour anesthetization period when

the bowls were kept at ambient seawater temperature. After anesthetization the anemones were removed and examind individually.

Counting and measuring acrorhagi

The fine fire polished tip of a bent pasteur pipette was used to fold back the limp tentacles and capitulum of the anesthetized anemones, exposing the acrorhagi which lie in the channel-like fosse at the top of the column. The total number of acrorhagi was recorded for each individual collected.

Acrorhagus size was determined for some of these anemones. If an anemone had fewer than 25 acrorhagi, all of these were removed and measured. If it had more than 25 acrorhagi, sometimes all, but usually every fourth one was removed and measured. The acrorhagi were first excised using iridectomy scissors and then placed on a glass slide with enough anesthetizing medium to barely float the coverslip. Because of their shape (Fig. 2) the acrorhagi always flattened laterally beneath the covership, with folds parallel to their long axes. The widths at the widest part of the white tip and the lengths from the acrorhagus tip to the base of the atrich-bearing ectoderm were measured at 350 ×.

There are several reasons for measuring only the nematocyst-laden tips of the acrorhagi: first, this is the area actually involved in inflicting damage during aggression; secondly, there is no other discrete division between the acrorhagus and the fosse; and thirdly, the basal portion of the acrorhagi is very thin and extensible, stretching greatly with an increase in internal fluid pressure (Fig. 2) and wrinkling and folding more after excision than the thicker ectoderm at the tip. The flattened tips of the acrorhagi are roughly elliptical, and acrorhagus area is accordingly approximated as twice the area of an ellipse with the major and minor axes measured as described above.

The photographs (Fig. 2) were taken in a tidepool at Eagle Point, Washington. To initiate the aggressive response, the tentacle tips of the anemones were repeatedly touched with a tentacle excised from a non-clonemate. The anemones were photographed at the same phase of the response (with the oral disc raised during the movement of application; Francis, 1973b) and are shown to the same scale (approximately 2.5 ×).

Reproductive state

Anemones were collected in the SIO preserve area and examined for the presence of gonads in mid-June (1975) when the gonads should be well developed (Ford, 1964). While the anemones were anesthetized, the presence or absence of gonads was determined by making a long incision in the surface of the pedal disc and examining the exposed mesenteries. Female gonads were brownish pink and male gonads were yellowish white. When uncertain, I excised pieces of mesentery and examined them microscopically for the presence of gametes. Most of the animals treated in this way recovered completely when returned to flowing sea water.

These anemones also reproduce asexually by longitudinal binary fission, and one often finds on their columns vertical scars that probably represent incomplete

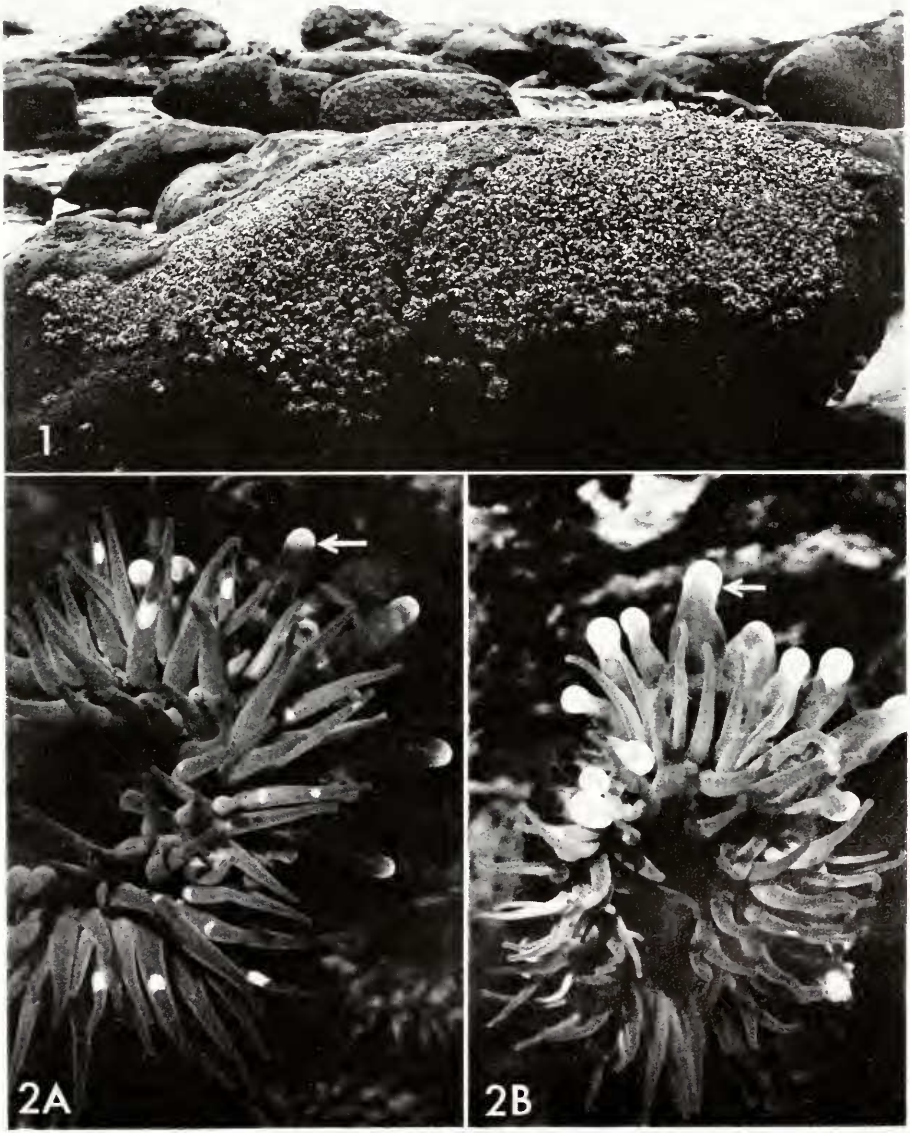

FIGURE 1. Boulders surrounded by sand (March, 1975) in the intertidal, Scripps preserve area, La Jolla, California. In the foreground clonal aggregations 201 and 202 are separated by a conspicuous anemone-free space. The other borders of the aggregations are free of intraspecific competition.

FIGURE 2. Two genetically identical anemones (approximately 2.5 ×) performing the aggressive response in a tidepool at Eagle Point, San Juan Island, Washington. The fully inflated acrorhagi (arrow) of the midclonal anemone (A) are much smaller and more sparse than those of a much smaller clonemate from an interclonal border (B).

healing of a relatively recent division. The animals collected to assay gonad development were also examined for the presence of fission scars.

Wet weight determination

Wet weight was used as an index of individual size that is independent of differences in body composition and readily determined without damage to the animals. To minimize random variation in the fluid content of the coelenteron, the anesthetized anemones were gently squeezed and blotted with damp absorbent paper. They were then weighed to the nearest 0.1 g on a top-loading balance.

Sampling

Comparing animals from different locations within the same clonal aggregation eliminates variation due to genetic differences and isolates positional effects. Samples from each clone included: all of the animals from a border adjacent to another clonal group (the interclonal edge); at least an equal number of individuals from a border roughly parallel with the interclonal edge and free of contact with nonclonemate conspecifics (the free edge); and at least as many anemones taken in rows roughly parallel to the interclonal border and a minimum of 10 cm from either the free border or the interclonal border (midclone). To avoid differences in the period of daily tidal exposure and/or seasonal sand burial between the sample groups within each clone, care was taken to collect all three samples from approximately the same tidal heights. To assure that the sampling was not biased, the clones were chosen and the samples collected during tidal exposure when the animals were contracted, making it impossible to see the acrorhagi. Unless specifically noted, all of the data collected are reported here.

Most of the samples were collected at La Jolla, California in the Scripps Institute of Oceanography (SIO) preserve area between the Scripps pier and Black's Beach. This area was particularly suitable because the clonal aggregations meet the criteria outlined below, being closely packed and isolated on the open faces of large boulders that are surrounded by sand (Fig. 1). For comparison, samples were also taken in Puget Sound at Eagle Point on San Juan Island, Washington, where the anemones are limited to crevices and tidepools, rather than colonizing boulder faces.

Several criteria were used in selecting the clones to be sampled. The clonal aggregations were as large as possible and quite tightly packed. Both of these circumstances minimize the likelihood of mixing between the groups sampled within each clone and thus accentuate positional differences. Further, the aggregations were relatively isolated from neighboring clones, except at one (SIO preserve area clones 201, 205, 209 and 223; and Eagle Point clone 223) or more (SIO preserve area clones 213, 216, 218, 221 and 222) well defined interclonal borders no more than 3 cm wide. This increases the likelihood that interclonal contact was occurring and had been limited to a narrowly defined area of the group. Finally, whenever possible the aggregations selected had an unobstructed, competition-free edge (*i.e.*, an edge of the clonal aggregation roughly opposite the interclonal border and free of neighboring conspecifics).

TABLE I

Relationship of individual size to position within the aggregation: mean wet weight (grams) ± their standard errors, and sample size.

Identifying number for each clone and (sampling date)	Position within the aggregation		
	Midclone mean ± s.e. (N)	Free edge mean ± s.e. (N)	Interclonal edge mean ± s.e. (N)
211 (IV/75)	0.74 ± 0.07 (10)	0.52 ± 0.04 (10)	none
221 (VI/75)	0.91 ± 0.09 (26)	none	0.48 ± 0.06 (16)
222 (VI/75)	1.12 ± 0.07 (20)	none	0.82 ± 0.11 (12)
223 (X/75)	0.54 ± 0.06 (27)	0.37 ± 0.05 (15)	0.38 ± 0.07 (27)
201 (III/75)	0.71 ± 0.08 (8)	0.50 ± 0.07 (8)	0.63 ± 0.12 (10)
205 (III/75)	1.11 ± 0.12 (30)	0.75 ± 0.08 (10)	0.74 ± 0.05 (10)
209 (III/75)	1.28 ± 0.20 (10)	1.04 ± 0.08 (9)	1.11 ± 0.14 (9)
216 (VI/75)	0.86 ± 0.16 (9)	0.69 ± 0.12 (7)	0.70 ± 0.16 (7)
grouped 201, 205, 209 & 216	1.01 ± 1.08 (37)	0.76 ± 0.05 (34)	0.79 ± 0.06 (36)

For comparison, samples were also taken from a clone apparently isolated from other conspecifics. SIO clone 211 rested in a shallow depression of a large, bare boulder; the nearest neighbors were 23 cm from the aggregation.

RESULTS

Individual size and position within the aggregation

Wet weights are reported for anemones collected without size bias from at least two of the three standard locations (interclonal edge, free edge, and midclone) in eight separate clones. Some of the samples collected specifically to determine reproductive state were deliberately biased toward larger specimens, and those data are not included here.

Means and their standard errors for each group are shown in Table I. Since the samples taken from each clone were small, means and their standard errors were also calculated by grouping the data from the four La Jolla clones for which complete information is available (Table I). Sample sizes for the clones were similar except in one case; the midclone sample ($N = 30$) for clone 205 includes animals taken in three separate vertical rows. Only one (the most central) of these subsamples was included in calculating mean and standard error for the grouped data.

Number of acrorhagi per individual and position in the aggregation

Samples were taken at the standard locations in each clone and the anemones were returned to the laboratory where they were anesthetized and their acrorhagi

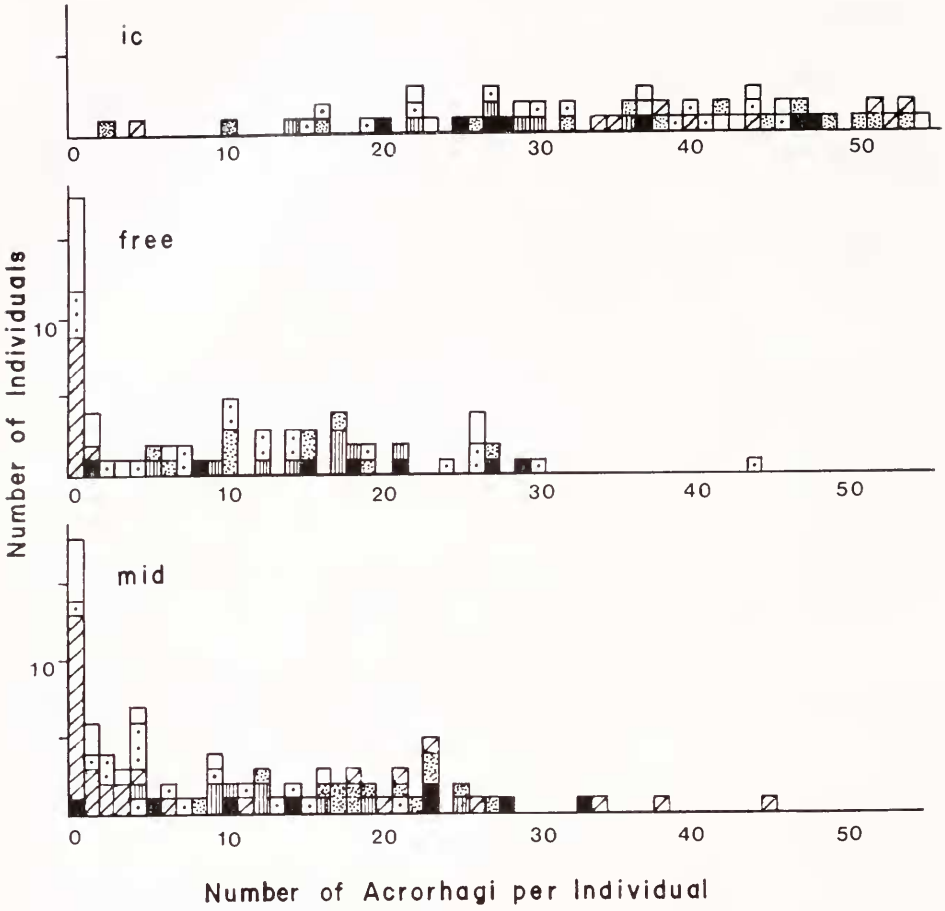

FIGURE 3. Number of acrorhagi per individual for anemones sampled from three different positions within each clone: an interclonal border (ic), a border free of intraspecific competition (free), and the middle of the clone (mid). The six clones sampled are clones 201 (dot), 205 (slash), 209 (open square), 213 (upright lines), 216 (black square), and 218 (stipple).

counted. The number of acrorhagi per individual is shown for each individual taken from the six La Jolla clones for which there is complete data (Fig. 3).

Means and their standard errors for these grouped data are shown in Table II. Since the samples from the clones were somewhat unequal, the means for each location in each of the six clones (Table II) were also calculated and from these, the mean of the means and their standard errors for each position: 1) midclone anemones, 11.1 ± 2.46, $(N = 6)$; 2) free edge anemones, 10.6 ± 2.62, $(N = 6)$; and 3) interclonal edge animals, 33.7 ± 1.43, $(N = 6)$.

Also included in Table II are data from a small isolated clonal aggregation

(without an interclonal border; clone 211) and two aggregations without competition-free borders (clones 221 and 222).

An appropriate correction for size variation could be made by dividing the number of acrorhagi per individual by the cube root of the individual wet weight. This correction greatly reduced the variance when applied to data collected from a large, apparently isolated aggregation from Eagle Point, Washington (unpublished data). Since the interclonal border anemones tended to be smaller than midclone anemones from the same clone (Table I), correction for size would emphasize the already apparent difference between the two groups. I have chosen instead to present the data in their simplest form.

Acrorhagus size and clonal position

Anemones from two of the clones sampled for acrorhagus number were also sampled to determine acrorhagus size. Differences in acrorhagus size are easily observed during the aggressive response (Fig. 2) and were readily apparent when the anesthetized anemones were examined to count their acrorhagi. However, the particular clones and individuals chosen for sampling and for the field photograph were selected haphazardly.

Figure 4 shows the area in mm^2 of all acrorhagi excised from anemones in the

TABLE II

Number of acrorhagi and individual position within the aggregation: means ± their standard errors and sample size.

Identifying number for each clone and (sampling date)	Position within the aggregation		
	Midclone mean ± s.e. (N)	Free edge mean ± s.e. (N)	Interclonal edge mean ± s.e. (N)
211 (III/75)	0.4 ± 0.16 (10)	4.2 ± 2.43 (10)	none
221 (VI/75)	6.6 ± 1.14 (19)	none	39.7 ± 3.93 (12)
222 (VI/75)	6.6 ± 0.99 (23)	none	27.8 ± 2.79 (16)
223 (X/75)	1.8 ± 0.65 (27)	2.6 ± 1.06 (15)	16.7 ± 2.56 (27)
201 (III/75)	6.6 ± 1.35 (14)	13.8 ± 3.25 (16)	31.0 ± 3.52 (11)
205 (III/75)	8.1 ± 2.38 (30)	0.1 ± 0.10 (10)	38.4 ± 4.67 (10)
209 (III/75)	3.4 ± 1.66 (10)	5.4 ± 2.82 (12)	35.1 ± 3.98 (9)
213 (VI/75)	13.7 ± 2.03 (10)	14.4 ± 1.67 (9)	28.6 ± 3.44 (7)
216 (VI/75)	15.6 ± 3.89 (9)	16.9 ± 3.89 (7)	33.1 ± 4.17 (7)
218 (VI/75)	19.2 ± 1.44 (14)	13.4 ± 1.60 (13)	35.7 ± 4.42 (14)
grouped 201, 205, 209, 213, 216 & 218	10.6 ± 1.13 (87)	10.6 ± 1.25 (67)	34.4 ± 1.71 (58)

various positions in both clones (open squares) and the mean acrorhagus tip area for each individual animal (large dots).

The mean acrorhagus size (acrorhagus tip area in mm^2) for each individual has been used to calculate means and their standard errors for each group: 1) clone 216—interclonal edge animals, 12.9 ± 2.34, $(N = 7)$; 2) clone 216—free edge animals, 2.2 ± 0.60, $(N = 6)$; 3) clone 222—interclonal edge animals, 11.6 ± 1.34, $(N = 8)$; and 4) clone 222—midclone animals, 3.3 ± 0.55, $(N = 8)$. Again these data are presented in their simplest form in preference to including a correction for the size variation among individuals.

Gonad development and individual position in the aggregation

Gonad development in this species is seasonal and size-related (Ford, 1964; Francis, 1973b); the animals were collected during the pre-spawning period and the data are reported as gonads present or absent for animals of specific sizes (wet weights). My own previous work as well as the present data clearly indicate that the lower size limit for sexual reproduction varies among clones. Larger samples

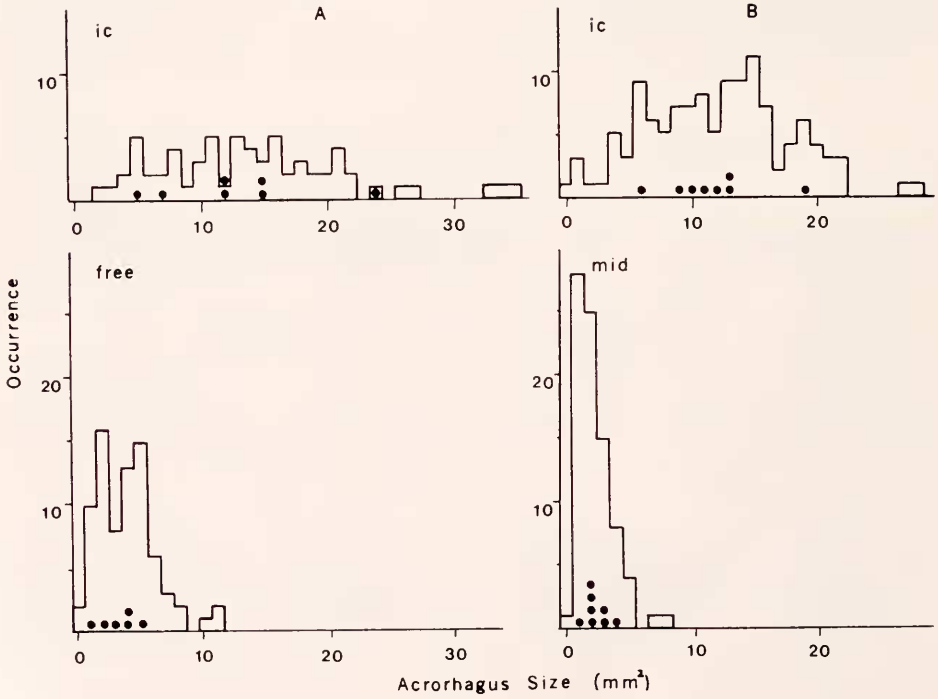

FIGURE 4. Size (mm^2) of each acrorhagus measured (bar graph) for anemones from different positions within clones 216 (A) and 222 (B); and average acrorhagus size per individual (dots) calculated from the same data. Anemones were collected from interclonal borders (ic), borders free of intraspecific competition (free), and the middle of the clones (mid).

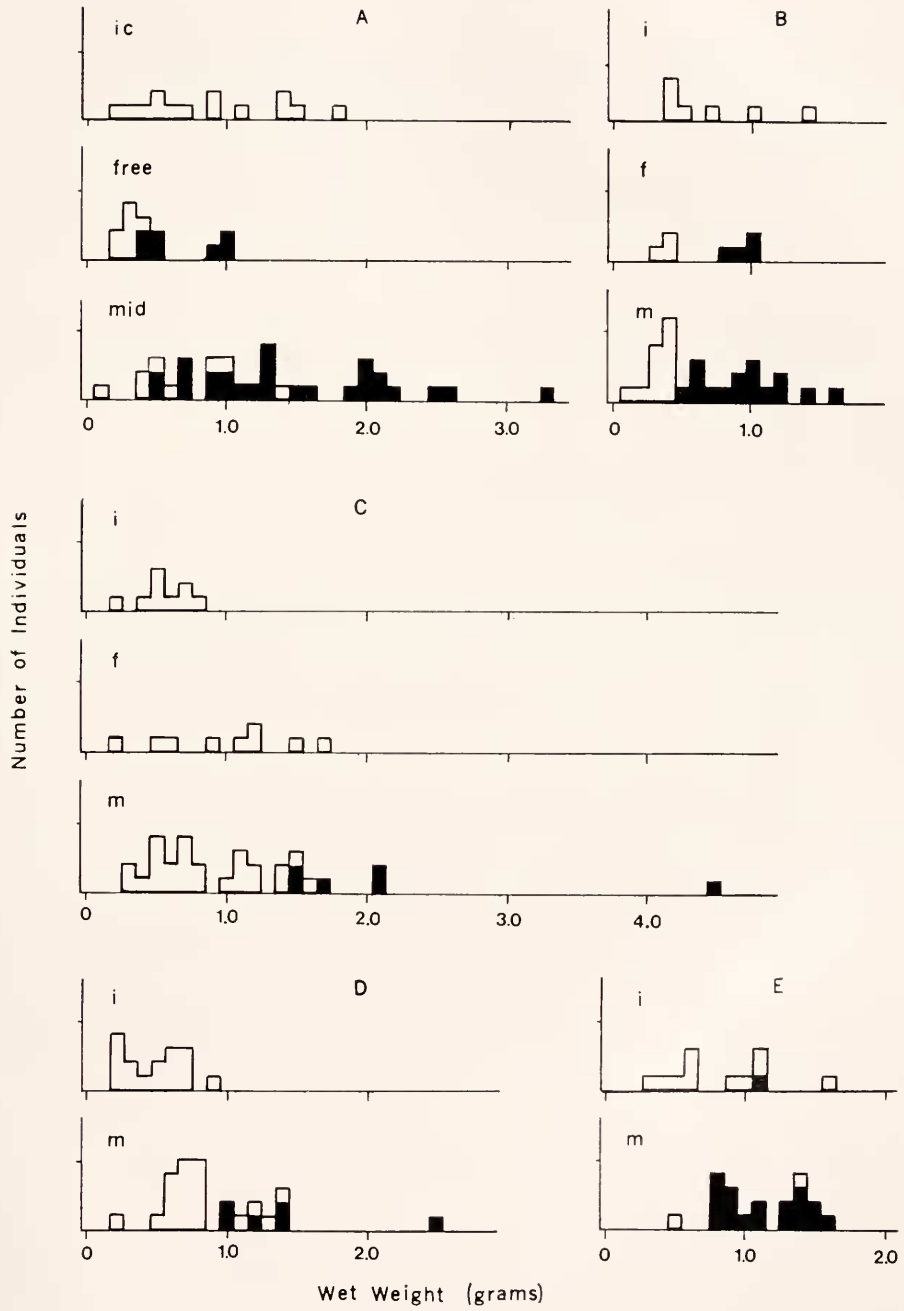

FIGURE 5. Presence of gonads (black square) or absence of gonads (open square) as a function of size (wet weight in grams) for anemones sampled from different positions (ic represents interclonal border; f, border free of intraspecific competition; and mid, midclone) within clone 218 (A), 216 (B), 213 (C), 221 (D), and 222(E).

TABLE III

Incidence of fission scarring and individual position within the aggregation: number of individuals scarred/number examined, and percent scarred.

Identifying number for each clone and (sampling date)	Position within the aggregation		
	Midclone	Free edge	Interclonal edge
221 (VI/75)	3/26 = 12%	none	0/12 = 0%
222 (VI/75)	1/20 = 5%	none	0/16 = 0%
213 (VI/75)	10/23 = 43%	5/9 = 56%	2/9 = 22%
216 (VI/75)	5/28 = 25%	1/7 = 14%	1/7 = 14%
218 (VI/75)	11/28 = 25%	5/11 = 45%	2/13 = 15%
grouped 213, 216 & 218	26/79 = 33%	11/27 = 41%	5/29 = 17%

were therefore taken from the middle of each aggregation to establish the limit for the clone, and the data for each clone is presented separately (Fig. 5). Samples from midclone and from the free edges of clones 213 and 218 were biased toward larger animals to increase the likelihood of collecting animals over minimum reproductive size. Of the five clones sampled only clone 222 was male; the rest were female.

Of the 42 anemones collected from interclonal borders, only one had gonads, and these were few and small. Eleven of the 46 free edge animals had developed gonads, and 73 of the 140 midclone anemones sampled had gonads. Since many of the edge animals were below minimum reproductive size, it is reasonable to compare the number of animals in each location that are above the minimum reproductive size for their clone. Of the 22 anemones from an interclonal edge that were larger than the smallest sexually developed individual collected from the same clone, only one had gonads. Eleven of the 14 anemones over minimum reproductive size from the free edge were ripe, and 73 of the 83 specimens over minimum reproductive size from midclone were ripe. A chi-square test using a two by three contingency table shows significance at above the 99.5% confidence level for either analysis.

Asexual reproduction and individual position in the aggregation

Table III shows the occurrence of fission scars on the columns of animals collected during June, 1975 and examined for scars. Complete information was available for three of the clones. When these data are grouped by position, a chi-square analysis using a two by three contingency table indicates that the apparent differences among the positional groups might be expected to occur by chance one time in twenty.

Inequalities in binary fission

"Daughter" pairs resulting from asexual divisions that occurred in the laboratory were weighed as soon as possible after fission to determine the equality of these divisions. The wet weight in grams for the larger of the two halves and the percent of the original individual that this represents are arranged here from the most to the least equally divided: 1) 0.86 g (51%); 2) 0.37 g (51%); 3) 0.31 g (53%) 4) 1.37 g (53%); 5) 1.06 g (55%); 6) 0.31 g (56%); 7) 2.64 g (58%); 8) 0.36 g (63%); 9) 7.22 g (63%); 10) 0.96 g (68%); and 11) 0.45 g (75%).

Discussion

From these results it is apparent that the warrior anemones living at an interclonal border have more and larger acrorhagi than do their clonemates either at an edge free of intraspecific competition or in the midst of an aggregation. The striking lack of gonads among the warriors during the prespawning period might indicate that they spawn earlier than their clonemates or that they develop gonads and spawn later; however it seems more likely that border warriors usually fail to develop gonads at all. The rate of asexual reproduction (as indicated by the incidence of fission scars) may be lower among the fighting anemones than among the nonfighters, both those in the midst of aggregations and those at edges free of intraspecific competition. There is no apparent difference in the size of interclonal edge warriors as compared with free edge animals; however midclonal anemones are larger on an average than their clonemates at either edge of the group. All of these differences except the size difference are clearly related to the intraspecific aggressive behavior. Some of the implications of this situation bear further discussion.

For animals that reproduce asexually, the term *individual* is ambiguous; for a recent discussion, see Mackie, 1973. *Anthopleura elegantissima* reproduces asexually by binary fission, so one anemone is only temporarily distinguishable from its clonemates. It was formerly part of other now-fragmented anemones and will presumably continue to fragment indefinitely. With this explicitly understood, I shall continue to use the term *individual* to mean one temporarily distinguishable physical entity, the term *clone* to denote the genetic entity, and the terms *aggregation* and *clonal group* to identify a contiguous group of genetically identical anemones.

Without entirely sacrificing the genetic plasticity available through sexual reproduction, the clonal aggregating form of *Anthopleura elegantissima* has invested in an evolutionarily conservative life style involving longevity, indeterminate growth and asexual reproduction. For many organisms the sexual adult is a temporary vehicle for an evolutionarily plastic and potentially immortal genome. Longevity, and perhaps even immortality for the entire organism, is a reasonable strategy in a stable environment that is either unvarying or (like the intertidal) predictably varying. This requires that the organism be capable of extensive repair and regeneration.

Asexual reproduction in its simplest form, fragmentation, is also available only to organisms with a high capacity for repair and regeneration. With asexual

reproduction, a genetic entity can grow indefinitely without the mechanical problems inherent in unlimited increase in individual size. Furthermore, a genotype dispersed as a number of separate individuals (*i.e.,* a clone) is less liable to be exterminated, a serious problem for the competitive immortal.

Unless external factors such as predation or environmental instability effectively limit population size, intense competition is inevitable among immortals that reproduce sexually and are capable of indeterminate growth.

There are two rather different ways to consider the connection between genetic similarity and intraspecific interactions. It is reasonable to expect that the more closely related two individuals are, the more similar their requirements will be, and the more extensive their competition for resources in a resource-limited situation. On the other hand, if it is of advantage to cooperate with conspecifics, cooperation with a close relative will be especially advantageous evolutionarily because any benefits gained in this way increase the fitness not only of the genes that the individual itself carries but also of the common genes carried by the near relative.

Whether an animal responds to conspecifics in an interfering or a cooperative manner will depend on whether the advantages gained by cooperation outweigh those gained by excluding that competition.

The existence of a complex aggressive response directed against all nonclonemate conspecifics implies that intraspecific competition is quite costly for *Anthopleura elegantissima,* while the existence of the large clonal aggregations (Fig. 1) so common for this species and the specialization among individuals in these groups (reported here) imply significant advantage in cooperation under some circumstances. Probable advantages of living in aggregations as compared with solitary living include reduction of the effective surface area resulting in reduced water loss (Roberts, 1941) and reduced drag (M. Koehl, Duke University, personal communication), cooperation in holding larger food items, and physical exclusion of interspecific and non-clonemate intraspecific competitors. Although the overlap in requirements and capabilities among clonemates is obviously maximal, more is to be gained by cooperation with them than with any other genotype. Since members of an aggregation are genetically identical, an advantage gained by an anemone for any group member is an advantage to its own genotype; and pure altruism will have the same evolutionary effects as pure selfishness.

Animals that cannot distinguish near relatives from other conspecifics must choose between the benefits of interference and those of cooperation. The clonal aggregating form of *Anthopleura elegantissima* can benefit maximally from both types of interaction only because the individuals can distinguish clonemates from all other members of the species, (Francis, 1973b).

I argue first that intraspecific competition for space will be important for an animal like *Anthopleura elegantissima,* and further that the existence of the intraspecific aggressive behavior and the specialized equipment involved in intraspecific aggression is evidence that such competition actually is important. This leaves an implied question unanswered: what, if anything, prevents intense and wasteful competition among clonemates?

Colonial organisms (*i.e.,* organisms that maintain connections among clone

members) show coordinated and orderly growth and division resulting in regular spacing of the individuals and expansion of the colony. This is only possible because the resources of a colony can be transported to budding areas.

Binary fission in *Anthopleura elegantissima* produces separate, slow-moving individuals rather than an orderly array of interconnected individuals. Consequently, growth and asexual reproduction are not easily coordinated to accomplish orderly extension of the group as they are in colonies.

Over-crowding resulting in competition for space and/or food will be a problem within dense aggregations of any sessile organism if the individuals continue to grow independently. The anemones will continue to grow if food is available in excess of that required for maintenance and activities unless they stop feeding or use the energy to produce more gametes. It seems unlikely that the anemones will stop feeding when crowded; however, gonads have been observed to develop more than once a year (B. Jennison, University of California, Berkeley, personal communication). Since smaller animals have larger surface to volume ratios than larger animals of the same proportions, asexual reproduction among anemones in a crowded area will probably increase the combined pedal disc area and thereby worsen any crowding problem. It is not yet clear what factors control growth, fission or sexual reproduction.

Fredericks (1976) suggests that movement in response to oxygen gradients can effect spacing within aggregations of *Anthopleura elegantissima*. Nonetheless, a clonal group that continues to expand will eventually occupy all the suitable substratum available in a particular location and crowding will occur. When subject to adverse conditions in the laboratory, these anemones can detach and rapidly re-attach (personal observation; and K. Sebens, University of Washington, Seattle, personal communication). In the field I have occasionally found unattached individuals in tightly crowded tidepools. Detachment could serve as a dispersal mechanism for clones that have saturated the holding capacity of their immediate surroundings.

How might morphological specialization arise within a clonal aggregation? Barring somatic mutation, the individuals are genetically identical and of the same age, having arisen from the same zygote. Variation among clone members is possible only to the extent that genetic expression can be affected by the environment.

Within the phylum Coelenterata are species showing all degrees of colony organization and individual specialization. At one extreme, the Siphonophora have been described as super-organisms because the interconnected and highly polymorphic polyps are organized into well coordinated colonies with distinctive species-specific morphologies. At the other extreme, the sea anemones (Actiniaria) do not remain attached and until now were not known to show specialization or group organization.

The organization within clones of *Anthopleura elegantissima* described here is unique for the phylum, in being social (*i.e.*, involving separate individuals) rather than colonial (involving attached individuals). Ability to specialize and to coordinate is limited by lack of connection among individuals. Without gut connections between clonemates, each anemone must feed for itself. Without nervous,

neuroidal or circulatory connections with clonemates, and lacking a CNS and sophisticated light or sound receptors, each anemone must respond individually to its immediate surroundings. Any coordination of activity must involve either pheromones (Howe, 1975) or direct contact.

There are two different, although not mutually exclusive models that might explain the nonrandom arrangement of somewhat specialized individuals present in the clonal aggregations: *model one*—individual development during growth and regeneration might be affected directly by differences in microhabitat; and *model two*—unequal divisions and imperfect regeneration could produce variation within a clone, and individual success might then depend on microhabitat.

The data for sexual reproduction in relation to clonal position (Fig. 5) are most easily interpreted using the first model. The specific hypothesis I am presently testing is that the interclonal border warriors use enough energy in intraspecific aggression that they lack energy reserves for gamete production.

The lower fissioning rates of the warriors as compared with free edge or midclone animals (Table III) is probably also a result of their experience at the interclonal border (model one) rather than a variation favored by conditions at that location (model two). If there is insufficient energy for sexual reproduction among these animals, it is reasonable that growth rates and possibly also fission rates might be reduced. Coordination of growth rate and fission rate is necessary for control of individual size. Although it is not yet clear what factors are involved in triggering fission, the relationship is certainly not simply that animals reaching a certain size in each clone divide. The data given above for daughter pairs produced by fission include wet weights for four animals from the same clone (animals 1, 2, 3, and 8). Variation in size at the time of fission is considerable; wet weights of the pre-fission anemones were 1.70 g, 0.72 g, 0.59 g and 0.57 g, respectively.

There could be unequal success among animals of different sizes in particular locations. Fission alone will produce size variation within clones unless growth and division are synchronous. The range of such variation will be increased by inequalities in fission (documented here) and by shrinking of starved animals (Muscatine, 1961). In the crowded centers of aggregations, large animals might over-reach smaller clonemates and get more food, causing the larger anemones to get larger and the smaller ones to get smaller. At the edges of the clones, however, being small might not be such a disadvantage since the tentacles on one side of even small anemones will extend beyond the clone.

The acrorhagi of a given individual are usually asymmetrical in their arrangement (personal observation) and variable in size (Fig. 4, data collected separately for each individual, but grouped here); furthermore there is no apparent consistency among clonemates in their patterns of acrorhagus arrangement. Since fission is often unequal, this and the variation in acrorhagus number might be explained by failure of the anemones to replace some or all of the acrorhagi lost during fission. This explanation probably accounts for the variation in acrorhagus number among individuals from the middle of clones and from isolated clones (Table II).

Might position-related differences in acrorhagus size and number be a matter of differential success of diverse morphological types arising randomly in this way;

that is, can this situation be described using model two? If interclonal border anemones have more and larger acrorhagi only because anemones with little weaponry cannot long survive at that location, the variance for both acrorhagus size and the number of acrorhagi per individual should be reduced at that location. The variances are consistently higher, not lower, among the warriors than among their clonemates (Table II and Fig. 3). Furthermore, the sample means for the warriors are at the extremes of variation for the other clone members sampled (*c.f.*, Fig. 3 and Table II; Fig. 4 and the data in the corresponding text). To explain these data using only model two it is necessary to postulate not only selection at the interclonal borders favoring the warrior morphology, but also selection at midclone and free edges favoring animals with reduced weaponry. These data are perhaps more easily interpreted using model one or a combination of the two models. The hypothesis presently being tested is that anemones at the interclonal borders produce more and larger acrorhagi in response to their experience there.

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Summary

The aggregating form of the anemone *Anthopleura elegantissima* often lives in closely packed groups composed of genetically identical individuals. These clonal aggregations remain separated from each other because contact between non-clonemates elicits intraspecific aggression (Francis, 1973a & b).

Since the anemones live in a dependable environment, are long-lived, have indeterminate growth, and reproduce sexually and asexually, and since predation does not appear to be severe, intraspecific competition for space is quite important. The ability to distinguish clonemates from non-clonemates allows the anemones to benefit from group living while interfering with all other conspecific competitors. A high proportion of the costs of this intraspecific aggression is paid by the anemones living at interclonal borders.

The interclonal border warriors have more and larger acrorhagi (specialized structures used in intraspecific aggression) than clonemates elsewhere in the aggregation and were without gonads in June when many of their clonemates were ripe. They are smaller on an average than midclone anemones but not smaller than clonemates from an edge of the aggregation remote from other clones. In the field, the fission rates of warrior anemones is not higher, and may be lower than that of clonemates in other parts of the same aggregation. Lack of gonads, small size, and low fission rates probably indicate that the warriors have less energy available for growth and reproduction than do their clonemates away from the battle zone.

Without physical connections among the individuals, the ability to coordinate and communicate is limited. Each anemone responds to its particular circum-

stances, and in so doing may fortuitously benefit its clonemates. Natural selection acts on the genotype (the clone). This is a very simple form of social organization both functionally and evolutionarily.

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